Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

THE INFLUENCE OF THE SEED UPON THE SIZE OF THE FRUIT IN STAPHYLEA. II

J. ARTHUR HARRIS

(WITH ONE FIGURE)

IV. On the nature of the correlation between the number of seeds and pod length

Heretofore we have contented ourselves with such analysis of our data as is necessary to the establishment on a sound quantitative basis of the fact of a correlation between the number of seeds developing and the length of the pod. This correlation is that of the statistician, not of the physiologist. It shows the existence of a relationship between two characters and measures its intensity. It does not prove that this relationship is due to a direct physiological interdependence between the two characters. To demonstrate such physiological interdependence one must remove the influence of other possible factors. All of the factors which seem possible sources of the correlation between the number of seeds developing and pod length and which can be investigated on the available data are discussed below.

I. THE HYPOTHESIS OF THE INFLUENCE OF THE RELATIONSHIP FOR OVULES AND LENGTH

As emphasized in the paper on *Cercis*, one of the sources of confusion in interpreting an observed r_{ls} is the fact that both l and s may be correlated with o, and so differences in the fruit length (l) which appear to be due directly to the number of seeds developing may be merely resultants of the relationship r_{lo} and r_{os}, and so indicate no physiological relationship between s and l. But it has been conclusively shown that $r_{ls} > r_{lo}$, thus demonstrating that the interdependence for seeds and length is not solely dependent upon the relationship for ovules and length. Indeed, it is only when both r_{lo} and r_{os} are high that they will greatly affect r_{ls}. It seems desirable, however, not to leave the question without showing just how much influence may be attributed to this factor. I use the two methods suggested in the paper on *Cercis*, namely, the correlation for length and seed/ovule index and the partial correlation coefficient. Comparing r_{ls} and r_{li} for the combined series we have:

Relationship	1906—2050 pods	1907—1218 pods
Number of seeds and length, r_{ls}....	0.3522±0.0131	0.2019±0.0185
Seed/ovule index and length, r_{li}....	0.3418±0.0132	0.2018±0.0185
Difference, $r_{ls}-r_{li}$............	0.0104±0.0186	0.0001±0.0261

Both differences are less than their probable errors, and of no significance.[1]

Consider now the correlation between s and l for constant values of o, as measured by the partial correlation coefficient of ρ_{ls}. The correlations for number of ovules formed and number of seeds developing per locule (r_{os}) are necessary. The tables of data are 36 in number, and since they are supplementary rather than fundamental to our main subject, we need not publish them. The constants with their probable errors are set forth in tables XI and XII.

TABLE XI

Number of shrub	r_{os} Correlation, ovules and seeds	r/Er
11.......	−0.076±0.037	2.06
12.......	0.042±0.035	1.19
13.......	0.154±0.037	4.16
14.......	0.112±0.038	2.96
15.......	−0.131±0.037	3.54
16.......	−0.063±0.039	1.61
17.......	0.080±0.039	2.05
18.......	0.002±0.039	0.05
19.......	−0.038±0.039	0.96
20.......	0.045±0.037	1.20
21.......	−0.094±0.039	2.40
22.......	0.028±0.039	0.71
23.......	0.014±0.039	0.36
24.......	0.144±0.038	3.78
25.......	0.078±0.039	2.00
26.......	0.026±0.039	0.67
27.......	0.048±0.039	1.22
28.......	0.093±0.038	2.45
29.......	0.058±0.039	1.48
30.......	0.042±0.039	1.08

TABLE XII

Number of shrub	r_{os} Correlation, ovules and seeds	r/Er
11.......	0.156±0.060	2.60
17.......	0.021±0.054	0.39
19.......	−0.072±0.046	1.56
24.......	0.159±0.038	4.23
29.......	0.028±0.047	0.60
31.......	0.057±0.038	1.50
32.......	0.094±0.043	2.18
33.......	0.126±0.126	3.19
34.......	0.025±0.025	0.56
35.......	0.079±0.079	1.73
36.......	0.150±0.049	3.08
37.......	0.004±0.040	0.10
38.......	0.033±0.040	0.82
39.......	0.137±0.059	2.33
40.......	0.045±0.039	1.16
41.......	0.010±0.050	0.19

---

[1] Possibly we are not quite justified in using the ordinary method of calculating the probable error of a difference here, that is, the square root of the sum of the squares of the two probable errors, but the differences in the correlation are so very small that it makes no practical difference.

In 1906, 15 of the constants have the positive and 5 the negative sign; in 1907, only one of the 16 is negative. Throughout, the values are too low to be of any practical significance. The mean for 1906 is 0.0282, and for 1907 it is 0.0658. We have already found low values for r_{lo}, and with the very small values for r_{so} just demonstrated, it seems hardly worth while to calculate ρ_{ls}. But, using the formula $\rho_{ls}=\frac{r_{ls}-r_{lo}r_{so}}{\sqrt{1-r_{lo}^2}\sqrt{1-r_{so}^2}}$, and substituting the mean values of the constants for the individuals as the most trustworthy measures for the physiologist, we find:

Relationship	1906—20 shrubs	1907—16 shrubs
Average r_{lo}	0.1282	0.1240
Average r_{so}	0.0282	0.0658
Average r_{ls}	0.3868	0.3636
Calculated ρ_{ls}	0.3865	0.3591
$r_{ls}-\rho_{ls}$	0.0003	0.0045

Obviously there is no practical significance whatever to be attached to the differences such as 0.0003 and 0.0045. In *Cercis*, r_{ls} is very materially reduced when allowance is made for the influence of the number of ovules. The two foregoing methods show that in *Staphylea* r_{ls} is essentially independent of r_{lo} and r_{so}.

2. THE HYPOTHESIS OF MECHANICAL STRETCHING

Where the seeds in a locule attain a considerable size and are numerous, it is quite possible that an increased size of the fruit might result from their space requirements, through the purely mechanical effects of crowding. In *Cercis* the seeds are relatively small and, generally at least, not in contact. Mechanical stretching seemed almost entirely excluded by the nature of the material, and I gave no attention to it. In *Staphylea* there seems even less reason to suppose this factor to be of any importance, but it is well to have such conclusions based on actual statistics. To test whether there is a sensible influence of the spatial requirements of the seeds upon the length of the pods, I think we may proceed as follows.

Clearly there can be little mechanical stretching of the placental space due to the development of a single seed in a locule. All the room which it demands is that necessary for its attachment; the pressure of adjoining seeds is a factor entirely removed. *Staphylea* has the advantage that the number of seeds developing is so small that it is easy to select material in which the stretching of the pod by a crowding of the seeds can hardly be a possibility. For pods with one to three seeds, there may be only a single seed in each locule, that is, seed formulae: 1–0–0, 1–1–0, 1–1–1. When more than three are produced, one of the locules must have two or more. Now the problem is simply this; given fruits producing the same number of seeds, are those in which two or more of the seeds are produced in the same locule larger than those in which but a single seed is produced in each locule?

TABLE XIII

CLASS	1906		1907	
	f	Mean length	f	Mean length
1 Seed				
1–0–0	960	5.57	519	6.26
2 Seeds				
1–1–0	291	6.39	227	6.83
2–0–0	204	6.46	105	6.96
3 Seeds				
1–1–1	57	7.23	32	7.19
2–1–0	172	6.97	117	7.21
3–0–0	47	7.21	26	6.96
4 Seeds				
2–1–1	64	7.56	40	7.38
2–2–0	33	7.39	15	7.33
3–1–0	39	7.90	23	7.61
4–0–0	14	7.64	5	7.80

Table XIII gives the number of pods available and the mean length of pod for the chief seed-formulae (including about 91 per cent of the whole number of fruits available) for the 1906 and 1907 series. The results are also shown graphically in fig. 5. Here the solid dots give the empirical means for the individual seed-formulae for 1906 and the circles those for 1907. The vertical lines (solid for 1906 and broken for 1907) indicate the mean length of pods with 1, 2, 3, and 4 seeds per pod, irrespective of the distribution of these seeds among the locules. Certainly there is no clear evidence in this figure that pods in which the seeds are grouped in less than three locules are longer than those in which they are as much distributed as possible among the three. It follows that mechanical

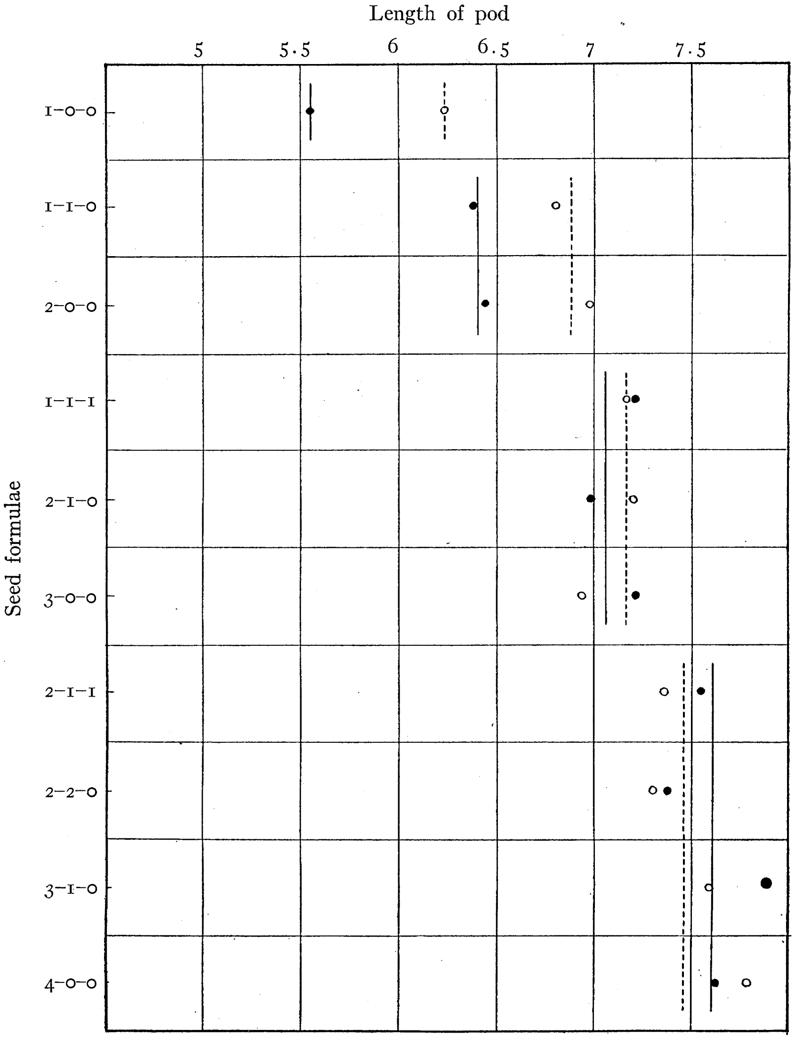

FIG. 5.—Mean lengths of pod for different seed-formulae and total number of seeds per fruit; solid dots and lines = 1906; circles and broken line = 1907.

stretching of the pod has had little or no part in the bringing about of the correlation between length and number of seeds developing.

3. THE HYPOTHESIS OF THE MUTUAL DEPENDENCE OF FRUIT LENGTH AND FERTILITY UPON OTHER CHARACTERS OF THE PLANT

Two characters both positively or negatively correlated with a third are correlated with each other. This is doubtless the source of much of the correlation found between organs. Possibly r_{lo} and r_{ls} indicate no physiological interdependence between l and o or l and s, but are due merely to l, o, and s being influenced by the position of the fruit on the inflorescence or by the number of pods per inflorescence. The correlation between the length of the pod and the distance of the flower-bearing node at which it is produced from the base of the inflorescence[2] is shown for the 1906 series[3] in table XIV, 1906, and for number of pods developing per inflorescence and length of pod in table XV, 1906. These give:

Position and length, $r_{pl} = -0.0580 \pm 0.0148$
Number and length, $r_{nl} = -0.1828 \pm 0.0144$

Statistically these values are certainly trustworthy, for $r_{pl}/E_r = 3.91$, and $r_{nl}/E_r = 12.70$. They indicate that both a more distal position on the inflorescence and a number of fruits above the normal is prejudicial to the maximum development of the fruit.[4]

If it be found that the number of seeds developing is also negatively correlated with the position and with the number of the

TABLE XIV, 1906

Position	LENGTH OF FRUIT									
	3	4	5	6	7	8	9	10	11	Totals
1.......	1	65	192	322	259	125	62	20	1	1047
2.......	4	50	167	197	143	88	31	9	..	689
3.......	1	25	69	75	54	31	14	2	..	271
4.......	..	2	9	13	6	4	5	1	..	40
5.......	..	..	...	3	...	...	...	..	..	3
Totals	6	142	437	610	462	248	112	32	1	2050

---

[2] The serial position of the node on the inflorescence counting from the base.

[3] Data for position are not available for 1907. Because of a severe frost many of the inflorescences produced only a single fruit, and it seems idle to study the number per inflorescence.

[4] Inflorescences with larger numbers of fruits will have more distally placed fruits. I have not worked out the correlation between these two characters, but if it is considerable the two constants just discussed are not independent, and probably one or both should be, biologically considered, more nearly 0.

TABLE XV, 1906

LENGTH OF FRUIT

Fruits in infl.	3	4	5	6	7	8	9	10	11	Totals
1......	..	..	..	..	1	..	..	..	..	1
2......	..	8	36	44	59	40	26	8	1	222
3......	1	22	85	167	127	66	41	8	..	517
4......	2	38	120	166	112	73	28	10	..	549
5......	1	40	90	115	88	42	7	2	..	385
6......	1	31	65	61	34	14	6	3	..	215
7......	..	2	20	20	21	7	4	1	..	75
8......	1	1	13	28	10	3	..	..	..	56
9......	..	..	2	2	4	1	..	..	..	9
10......	..	..	3	3	2	1	..	..	..	9
11......	..	..	..	..	..	..	..	..	..	..
12......	..	..	3	4	4	1	..	..	..	12
Totals	6	142	437	610	462	248	112	32	1	2050

fruits developing on an inflorescence, we should expect a positive correlation between number of seeds developing and length of pod, due to no direct physiological interdependence of the two, but solely to their correlation with these other characters. Turning to our data, we see the correlation surface for position and seeds per locule in table XVI, 1906, and between number per inflorescence and seeds per locule in table XVII, 1906. To the eye there seems to be little or no correlation. The calculating machine shows:

For position of fruit and seeds, $r_{ps} = -0.0148 \pm 0.0149$

For number of fruits and seeds, $r_{ns} = -0.0474 \pm 0.0148$

Again the signs are negative, but the values are so low that little importance can be safely attached to them.

With such low correlations, it seems hardly worth while to consider the amount of influence which position on the inflorescence or number of pods per inflorescence would have upon the degree of interdependence of s and l, but since biometricians are frequently criticized for neglecting just such biological considerations as this, I calculated the correlation for seeds and length for constant numbers of pods per inflorescence. Number rather than position was chosen, since the correlations are numerically higher and will have greater influence on r_{sl}. Working from the formula

$$\rho_{sl} = \frac{r_{sl} - r_{ns} \cdot r_{nl}}{\sqrt{1 - r_{ns}^2}\ \sqrt{1 - r_{nl}^2}},$$

we find:

$$r_{sl}=0.3522\pm0.0131,$$
$$\rho_{sl}=0.3498\pm0.0131,$$

$$\mathrm{r}_{sl}-\rho_{sl}=0.0024\pm0.0185$$

TABLE XVI, 1906

SEEDS PER LOCULE

Position	0	1	2	3	4	5	6	Totals
1............	1533	1109	355	115	33	11	..	3156
2............	1076	733	190	60	16	4	..	2079
3............	404	285	88	28	7	1	..	813
4............	56	40	12	9	2	..	1	120
5............	5	3	1	....	..	..	..	9
Totals.....	3074	2170	646	212	58	16	1	6177

TABLE XVII, 1906

SEEDS PER LOCULE

Fruits per infl.	0	1	2	3	4	5	6	Totals
1...........	2	....	1	....	..	..	..	3
2...........	299	238	82	29	14	4	..	666
3...........	761	556	170	54	15	4	..	1560
4...........	827	581	164	60	16	5	..	1653
5...........	591	399	120	37	7	1	..	1155
6...........	343	217	63	17	5	2	1	648
7...........	115	85	25	6	..	..	..	231
8...........	91	61	13	2	1	..	..	168
9...........	10	14	2	1	..	..	..	27
10...........	14	10	2	4	..	..	..	30
11...........	....	....	....	....	..	..	..	....
12...........	21	9	4	2	..	..	..	36
Totals.....	3074	2170	646	212	58	16	1	6177

The reduction in correlation is only about one-eighth of the probable error of the determination! Further arithmetic or discussion would be pedantic. I conclude that the correlation between the number of seeds developing and the length of the fruit is not merely a secondary result of the correlation of these two characters with position on the inflorescence or number of pods per inflorescence, but must be due to some force operating in the developing fruit itself.

For *Cercis* I have no data for the relationship between the number of pods per inflorescence and the fertility and length characters of the fruits, but it may be of some interest to determine the correlation between the number of ovaries and the number of ovules per ovary for the three series of intact inflorescences gathered in the spring of 1907.[5] The data for r_{no} are given in tables XVIII and XIX.[6] The coefficients of correlation[7] are

Tree 1, $r = -0.007 \pm 0.023$
Tree 2, $r = 0.030 \pm 0.021$
Tree 3, $r = 0.134 \pm 0.024$

In the first two cases the correlations are certainly insignificant. In the third tree there is a slight correlation which is about six times its probable error. Ordinarily this would be considered trustworthy, but the actual number of ovaries instead of the

TABLE XVIII, CERCIS

OVARIES PER INFLORESCENCE	TREE 1		TREE 2		TREE 3	
	Number of ovaries	Total ovules	Number of ovaries	Total ovules	Number of ovaries	Total ovules
5	...	...	5	27	25	125
6	6	44	...	...	112	532
7	84	647	...	...	139	672
8	197	1515	15	76	214	1043
9	176	1344	26	146	181	895
10	209	1585	130	679	49	243
11	142	1095	283	1495	11	60
12	47	359	297	1596	...	...
13	...	...	168	897	...	...
14	27	207	139	763	14	75
15	...	...	15	89	...	...
16	...	...	...	...	...	...
17	...	...	...	...	17	92
Totals	888	6796	1078	5768	762	3737

---

[5] HARRIS, J. ARTHUR, Is there a selective elimination of ovaries in the fruiting of the Leguminosae? Amer. Nat. **43**:556–559. 1909.

[6] Again the different inflorescence grades are necessarily weighted with the number of flowers which they bear, and the means and standard deviations used in determining the coefficients of correlation are calculated from these weighted frequencies. SHEPPARD's correction was not used. The single case of no ovules is probably due to one of the ovaries being still too young. In dissecting the ovaries out of the flowers, clearing, and examining under the lens, some accidents are unavoidable. There is no reason to believe that the 35 ovaries which were broken or ruined in clearing differed from those which could be counted. They are simply omitted in the calculations.

[7] Calculated by method described in Amer. Nat. **44**:693–699. 1910.

TABLE XIX, CERCIS

NUMBER OF OVULES PER OVARY

	0	1	2	3	4	5	6	7	8	9	10
Tree 1	..	..	..	..	3	1	49	279	476	76	4
Tree 2	1	1	5	32	177	327	431	100	4	..	..
Tree 3	..	..	10	23	198	341	179	11	..	..	..

number of inflorescences was used in calculating the probable error. This is perhaps justifiable, but had N been taken as 100, the actual number of inflorescences, the probable error would have been much higher, and in the third tree the correlation would have been only about twice or thrice its probable error. On the basis of available data, there is no demonstrable relationship, therefore, between the number of ovaries on an inflorescence and their characteristics.

4. THE HYPOTHESIS OF THE INDIVIDUALITY OF INFLORESCENCES

It has now been shown that neither position nor number of pods has sufficient relationship with the two characters immediately under consideration to produce a sensible correlation between them. Theoretically both p and n would influence, to some extent, the quantity of plastic material available for a given fruit, but so far as these evidences go, similarity of nutrition for both seeds and fruit wall has little influence in bringing about the correlation between them. These are not the only factors which might influence the food supply of a developing fruit. Some inflorescences may be much more generously supplied with fruit and seed building substances than others, and in the distribution of this material throughout the inflorescence, position of pod may have a negligible significance, and number of pods developing be of only small importance.

I believe the following method to be satisfactory in determining whether r_{ls} is due to the differentiation between the inflorescences of an individual either (*a*) in the capacity for development of the protoplasm of which their ovaries are made up, or (*b*) in the availability of food material for the expansion of these organs.

If both the pod length and the number of seeds developing are influenced by the nature of the inflorescence upon which they are borne, or by the quantity of the plastic material which it receives from the shrub, in a way to bring about a correlation between the length of a pod and the seeds which it matures when the pods from an individual are used as a sample, there should be a correlation between the number of seeds developing in a fruit and the length of another fruit on the same inflorescence. In short, if there is something inherent in the inflorescence which tends to influence both number of seeds developing and length of fruit in the same sense, so that a correlation arises between them, this influence should effect in some degree all pods with the result that the cross correlation between number of seeds developing in one pod and length of another pod should have a sensible positive value.

The only disadvantage of this method is its extreme laboriousness. It is necessary to draw up tables between the characters of the fruits of the same inflorescence, just as in a study of heredity one prepares tables showing the correlation between brothers in the same family. Each pod is used once in association with every other pod on the same inflorescence. The number of combinations thus secured will be $\frac{1}{2}n(n-1)$, and since for practical purposes we use each fruit once as a first and once as a second member of an associated pair,[8] we have for each inflorescence $n(n-1)$ combinations.

All inflorescences have not the same number of pods, and an inflorescence with six locules will give relatively fewer entries in the symmetrical table than one with twelve. I regret the necessity of thus giving weight to the larger inflorescences, but since the correlations between the number of pods per inflorescence and all the characters of the pod are generally very low, it hardly seems worth the labor to reduce all the inflorescences to a standard frequency to avoid weighting. Designating the two characters of a pair which are being compared as "first" and "second," and indicating them by one and two dashes respectively, we have the following relationships for consideration.

---

[8] For the intra-inflorescence relationship for the length of the fruit it is only necessary to draw up tables showing all possible combinations of the fruit lengths of the same inflorescence. But for ovules and seeds we are dealing with the individual locules, and there are three to each fruit. If we made every possible combination in the preparation of the tables, we would be correlating, in some cases, between the locules of the same fruit, and, in some cases, between the locules of different fruits on the same inflorescence. The point which we wish to get at is the relationship between the different fruits of the same inflorescence. The plan followed, therefore, has been to correlate the number of ovules formed or the number of seeds developing in each locule with the number in every other locule on the inflorescence, except those of the same fruit. In the same manner, in dealing with the relationships between length of pod and the fertility characters, the tables were so drawn as to show the relationship between the length of the pod and the fertility characters of all the locules on the inflorescence, except its own three.

Ovules of first locule and ovules of second locule, $r_{o'o''}$
Seeds of first locule and seeds of second locule, $r_{s's''}$
Length of first pod and length of second pod, $r_{l'l''}$
Length of first pod and ovules per locule in second pod, $r_{l'o''}$
Length of first pod and seeds per locule in second pod, $r_{l's''}$

Since the pods from each shrub must be treated separately, this requires the preparation of 100 correlation tables, containing some hundreds or thousands of entries each. These have been carefully prepared and verified, and the means and standard deviations used in obtaining the correlation coefficients calculated anew for all the characters from the weighted frequencies. The tables and constants are too bulky for publication. The end results

TABLE XX

INTRA-INFLORESCENCE CORRELATION COEFFICIENTS

Shrub	Ovules of first locule and ovules of second locule	Seeds of first locule and seeds of second locule	Length of first pod and length of second pod	Length of first pod and ovules per locule in second pod	Length of first pod and seeds per locule in second pod
11	0.516	0.098	0.517	−0.387	0.190
12	0.037	0.004	−0.003	−0.217	−0.091
13	0.078	−0.025	0.009	0.051	−0.008
14	0.093	−0.017	0.017	0.027	0.008
15	0.113	0.034	0.178	0.049	0.046
16	0.088	−0.009	0.113	0.083	−0.030
17	0.108	0.017	0.244	0.317	0.008
18	−0.026	−0.028	−0.045	0.020	−0.087
19	0.084	−0.017	−0.036	−0.068	−0.020
20	0.123	0.031	0.109	0.074	0.049
21	0.143	0.003	0.052	−0.067	0.000
22	0.026	0.020	0.059	0.007	0.039
23	0.084	0.015	0.018	−0.031	−0.014
24	0.093	−0.034	−0.007	0.010	−0.052
25	0.515	0.096	0.378	0.206	0.183
26	0.099	0.042	0.115	0.044	0.062
27	0.059	−0.038	0.058	0.117	−0.038
28	0.330	0.009	0.151	−0.029	−0.020
29	0.054	−0.009	0.197	0.044	0.034
30	0.185	0.003	0.124	0.026	−0.011

TABLE XXI

SUMMARY OF INTRA-INFLORESCENCE CORRELATION COEFFICIENTS

	OVULES AND OVULES		SEEDS AND SEEDS		LENGTH AND LENGTH		LENGTH AND OVULES		LENGTH AND SEEDS	
	f	Average	f	Average	f	Average	f	Average	f	Average
Positive...	19	+0.149	12	+0.031	16	+0.146	14	+0.077	10	+0.062
Negative..	1	−0.026	8	−0.022	4	−0.023	6	−0.133	10	−0.037
Total...	20	+0.140	20	+0.010	20	+0.112	20	+0.014	20	+0.025

appear in table XX, and these are still further summarized in table XXI.

The intra-inflorescence correlation for ovules is unquestionably positive, and perhaps high enough that one safely can say that the inflorescences are differentiated among themselves with respect to number of ovules produced. For number of seeds per locule the inflorescences seem not at all differentiated; it is not even possible to ascertain the sign of $r_{s's''}$, and its mean is only 0.010. This result seems to me of considerable physiological interest. I had expected to find a greater similarity among the numbers of seeds developing in the locules of the inflorescence than among the numbers of ovules formed. I thought that probably some inflorescences would be in much more advantageous positions for obtaining food material than others, and that in consequence the differences between inflorescences would be greater (and consequently the intra-inflorescence correlation higher) than for number of ovules. So far as we can judge from evidence at hand, the morphogenetic factor is stronger than the physiological[9] in determining the characteristics of the fruits of an inflorescence. For length, it seems reasonably certain that there is a slight similarity between the pods of the same inflorescence as compared with those of the tree in general.

---

[9] One must use extreme caution in such fields as this, for there are innumerable pitfalls. By morphogenetic I mean the organogenetic processes which give rise to the ovaries. By physiological factors I refer to (*a*) the ecological factors which determine whether an ovule shall receive a sperm, (*b*) to the availability of food material and other requisites for growth, (*c*) the innate vigor of the individual inflorescences which determine whether a fertilized ovule shall develop into a seed. The third of these is probably in some measure identical with the organogenetic. If (*a*) and (*b*) were really very different for the several inflorescences of an individual, one would expect the intra-inflorescence correlation for number of seeds to have sensible values and possibly to rise considerably above what it is for ovules. This is the case in *Sanguinaria* (Biometrika 7:328. 1910), where it seems that the main bulk of the

Finally, the results from the two correlations fundamental to our present purposes are unmistakable. The evenness of the division between positive and negative and the extremely low mean value of the coefficients $r_{l'o''}=0.014$ and $r_{l's''}=0.025$ prove that there is no material relationship between the length of one pod and the number of ovules or seeds in another pod of the same inflorescence. This seems to me to prove conclusively that there are no differences in the supply of plastic materials of the different inflorescences sufficient to account for both the number of seeds developing and the length of an individual fruit deviating from their means in the same way.

For *Cercis* I have no data for the mature inflorescence comparable with that for *Staphylea*. It is interesting, however, to compare the intra-inflorescence correlations for number of ovules in the ovaries collected at flowering time in the spring of 1907 with the results obtained for *Staphylea*. The data for $r_{o'o''}$ are given in table XXII.[10] The correlations are

Tree 1, $r=0.571\pm0.015$
Tree 2, $r=0.213\pm0.020$
Tree 3, $r=0.378\pm0.021$

Mean, $r=0.388$

These results indicate a differentiation among the inflorescences of an individual of *Cercis* somewhat higher than we have found in *Staphylea*, but three individuals are not sufficient for more than a suggestion. The finding of an intra-inflorescence correlation in another genus gives confidence in the results for *Staphylea*. Should

correlation between the placentae of the fruit is due to ecological and physiological factors. There, however, we were dealing with individuals subjected to an external environment, not with the several inflorescences of the same individual. Possibly (*a*) and (*b*) are optimum for all inflorescences, but only a small percentage of the seeds develop because of some internal limiting factor. The bladdery fruits are possibly adaptive, and too great a weight of seed would offset the advantage of the peculiar structural features.

[10] Calculations by method described in Amer. Nat., 1910, The "ovules of first ovary" gives the grade, and the "number of associated ovaries" gives the frequencies for both variables, the tables being symmetrical.

TABLE XXII, CERCIS

OVULES OF FIRST OVARY	TREE 1		TREE 2		TREE 3	
	Number of associated ovaries	Total ovules in associated ovaries	Number of associated ovaries	Total ovules in associated ovaries	Number of associated ovaries	Total ovules in associated ovaries
0	....	....	11	56	....	....
1	....	....	11	61	....	....
2	....	....	55	294	65	319
3	....	....	348	1891	168	854
4	21	163	1874	10096	1346	6594
5	7	55	3466	18422	2309	11330
6	409	3142	4600	24593	1358	6806
7	2322	17696	1118	6130	98	494
8	3984	30520	53	298	....	....
9	626	4813	....	....	....	....
10	27	214	....	....	....	....
Totals	7396	56603	11536	61841	5344	26397

an intra-inflorescence correlation for number of seeds and for length of pod be sometime demonstrated for matured fruits of *Cercis*, it would indicate that in this species a somewhat lower proportion of r_{ls} is due to a direct physiological relationship between the two characters than is indicated by the constants already calculated.

5. THE HYPOTHESIS OF THE DIFFERENTIATION OF INDIVIDUALS

If a sample of pods be made up of collections from a series of individuals, a (statistical) correlation will be found between two characters of the pod, say length and number of seeds, whether there is any physiological relationship or not, providing that the individuals are differentiated among themselves with respect to both of the characters in such a way that in the several individuals of the series both characters of the pair tend to fall above or below the means for all the individuals. Concretely, we understand for our present material that if, because of innate vigor or by reason of favorable environment, some individuals bore both larger pods and more seeds than the average, while other individuals with less innate vigor or with less favorable environment produced both smaller pods and fewer seeds than the average, then the correlation table prepared for the whole series of pods would show a sensible interdependence for length and seeds which would not be due to any direct physiological relationship at all, but solely to differentiation in the plants which produced them.

The criticism that the correlations for pod characters may be due to heterogeneity of material has already been met for the present study, by analyzing the data from each individual independently. To make assurance doubly sure, we may determine the correlations (*a*) between the mean length of the fruit and the mean number of ovules per locule (r_{lo}), and (*b*) between the mean length of the fruit and the mean number of seeds per locule (r_{ls}), for the individual trees. Working by the brute force method we get

1906	1907
$r_{lo}=0.004\pm0.150$	0.010 ± 0.168
$r_{ls}=0.418\pm0.124$	-0.371 ± 0.145

In both years r_{lo} is only a fraction of its probable error, and no significance whatever can be given it. Statistically, r_{ls} may be significant in both cases; for in 1906 $r/E_r=3.36$, and in 1907 $r/E_r=2.55$. Biologically the two constants, of roughly the same numerical order but opposite in sign, mean nothing except that mean length and mean seeds do not seem to be closely related. Probably both are determined by largely independent causes. The substantial quantitative results are due solely to the probable errors of sampling.[11]

[11] Reconsider in the light of these results the peculiar condition noted in table V, where it appeared that both r_{lo} and r_{ls} are lower for the population than for the mean values of these constants for the samples from individual trees. The explanation seems to be quite simple. The magnitude of r depends upon the largeness of the denominator, $\sigma_l\sigma_o$ or $\sigma_l\sigma_s$, as well as upon the numerator, $S(\mathrm{lo})$ or $S(\mathrm{ls})$, of the correlation formula. The mean $\sigma_{ls}\sigma_{os}\sigma_s$ of the individuals are seen in table V to be much lower than the same constants for the population. For both series the correlation between A_l and A_o is insignificant, and consequently we see a low value for r_{lo} for the population because of the high value of $\sigma_l\sigma_o$. This is also the tendency for r_{ls}, but in this case, the inter-individual correlation for A_l and A_s have material values which, although without biological significance because of their high probable errors, nevertheless have their influence upon the correlation constants for the population. In 1906, the inter-individual correlation is positive, and this tends to raise the population constant to about the same value as that for the mean of individuals, that is, 0.352 as compared with 0.387; but for 1907, the inter-individual correlation for means is negative and we find the discrepancy of 0.202 against 0.364. These results emphasize the importance of a stringently analytical treatment of data.

6. OTHER HYPOTHESES

The foregoing hypotheses have seemed the most reasonable ones to explain the relationship between the length of the fruit and the number of seeds developing, without the assumption of a direct causal relationship between them. All have given negative results in the sense that they have failed to show any reason for the interrelationship between length and number of seeds external to the two characters themselves. This does not prove that there is a direct causal relationship between them, that is, that their interdependence is not due to some outside influence, but I think that the factors suggested are the most important ones, and I have no data for taking up others on the present material.

We may conclude, therefore, with reasonable confidence, that the developing seed does in some way exert a developmental stimulus on the ovary wall. The nature of this stimulus must be ascertained by further studies.

V. Recapitulation

The chief problems, methods of reasoning, and conclusions from observations detailed both above and in an earlier paper on *Cercis*, may be briefly reviewed here.

That pollination is in many cases a stimulus to the development of the ovary now seems fairly well established. Several biologists have suggested that the developing seed also exerts an influence upon the growth of the fruit.

The establishment of this second hypothesis presents far greater difficulties than that of the first. So far as I am aware, no one has isolated bodies from the growing seed which when introduced into other ovaries accelerates development. Nor has it been proved that young ovaries with larger numbers of developing seeds show a higher rate of growth; and even if this were demonstrated, it would be impossible to say that the acceleration of growth was not due to the stimulation of an unusually large number of pollen tubes.

The most feasible method for a preliminary study seems to be to work with mature fruits and to ascertain whether the number of seeds may have had an influence in determining the size of the fruit. If the size of the fruit increases as the number of seeds becomes larger, the development of the seed must exert a stimulus to the development of the fruit wall, providing that the correlation between the number of seeds and the size of the fruit is not due to some other factor or factors upon which both seed number and fruit size are in some degree dependent.

The task is, therefore, twofold: (*a*) to obtain a measure of the correlation between the number of seeds and the length of the fruit, and (*b*) to show by a process of elimination that the correlation can, with a high degree of probability, be attributed to a direct physiological relationship between number of seeds and size of fruit.

I. The first of these undertakings is straightforward. The coefficients of correlation show that in both *Cercis* and *Staphylea* there is a very substantial interdependence between number of seeds and fruit length.

II. The second task is somewhat more complicated. The following facts indicate that this observed interdependence is due to physiological factors confined to the seed and ovary wall:

(1) In *Staphylea* the correlation between the total number of seeds and the length of the fruit is higher than that between the number per locule and length.

(2) The relationship between the number of seeds developing and the length of the pod is in large measure independent of the influence of the number of ovules.

(3) In both *Cercis* and *Staphylea* the possibility of a mechanical stretching of the fruit through the pressure of adjoining seeds seems to be excluded.

(4) Both length of pod and number of seeds developing are slightly correlated with the number of fruits per inflorescence and with the distance of the node from the base of the inflorescence, but the correlations are too low to be of any significance in producing the relationship between the number of seeds and length of pod.

(5) The inflorescences of a shrub of *Staphylea* seem to be slightly differentiated with respect to the number of ovules per locule and the length attained by the fruit. Apparently the inflorescences

are not at all individual in the number of seeds developing per locule in the fruits which they produce. The cross correlation coefficients for the number of seeds in one fruit and the length of another fruit of an inflorescence furnishes no indication that there are innate or environmental peculiarities of inflorescences which tend to influence both the number of seeds developing and the length of the fruit in the same direction. In short, one cannot explain the correlation between number of seeds and length as the result of superior innate vigor or favorable nutrition in some inflorescences of an individual and the contrary conditions in others.

III. From the immediately foregoing considerations, and from others detailed in the body of the paper, we seem to be justified in the conclusion that the measurable interdependence between the number of seeds and the length of the fruit in *Staphylea* and probably also in *Cercis* is a direct physiological one, and that the two characters stand in some degree in the relationship to each other of cause and effect.

While this conclusion has already been reached by some other biologists depending upon more general evidence, I believe that this and the preceding study are the first in which a fairly satisfactory approximation to proof has been attained. A chief value of these studies is that the numerous difficulties surrounding the problem have been more clearly realized than appears to have been done before. The numerical results, while substantiating in a satisfactory manner the conclusions drawn from them, must be looked upon as merely approximations.

CARNEGIE STATION FOR EXPERIMENTAL EVOLUTION
COLD SPRING HARBOR, N.Y.